Octopuses influence den selection by juvenile Caribbean spiny lobster

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Abstract.   Octopuses are notorious predators of crustaceans, yet knowledge of their interactions with lobsters is largely anecdotal. Whether by preying on juvenile lobsters or by competing with them for dens or bivalve prey, octopuses should influence the den selection and therefore spatial distribution of lobsters. Lobsters are chemosensitive, so if the interaction is strong, they may respond to chemical cues produced by octopuses and avoid dens or areas where octopuses dwell. In mesocosms, juvenile Caribbean spiny lobsters (*Panulirus argus*) avoided dens emanating octopus chemical signals. Field manipulations of artificial dens at several spatial scales (<0.1 m to 10 m) showed that the distribution of lobsters was significantly influenced by the proximity of octopuses. Lobsters were significantly less likely to inhabit dens within 2 m of an octopus den, but this strong negative effect disappeared when dens were 10 m apart.

Extra keywords: chemical cues, competition, *Octopus briareus*, *Panulirus argus*, predation, spatial distribution

Introduction

Predation strongly influences the life-history dynamics of juvenile Caribbean spiny lobsters, *Panulirus argus* (Marx and Herrnkind 1985a; Herrnkind and Butler 1986; Eggleston *et al*. 1990; Smith and Herrnkind 1992). Aside from decreasing the number of recruits available for subsequent life stages (see Butler and Herrnkind 2000), predation may indirectly affect the behaviour of juvenile spiny lobsters and their choice of habitats or shelters (Childress and Herrnkind 1994; Butler *et al*. 1997).

In Florida Bay, spiny lobsters exhibit three behavi*o*urally and ecologically distinct phases after settlement: algal (5–15 mm CL), transitional (16–25 mm CL), and postalgal (26–35 mm CL) (Smith and Herrnkind 1992). Early benthic stage (algal phase) juveniles initially settle and shelter within beds of the red macroalga *Laurencia* spp. (Marx and Herrnkind 1985b; Butler *et al*. 1997), where they have abundant prey and are provided substantial refuge from predation. Transitional juveniles occupy both macroalgae and crevice shelters; the size at which they emerge from settlement habitat and seek crevices depends on shelter availability, presence of conspecifics, and perhaps the presence of predators (Childress and Herrnkind 1994). Postalgal juveniles occupy small crevices provided by sponges, coral heads, solution holes, and other structures (Smith and Herrnkind 1992). These ontogenetic shifts in sheltering behavi*o*ur reflect the changing predation risk that juvenile lobsters face after initial settlement. Their dependence on shelter is strong and driven by predation pressure.

To date, all studies of predation and shelter use patterns of spiny lobsters have focussed on piscine predators (Chittleborough 1975; Herrnkind and Butler 1986; Howard 1988; Eggleston *et al*. 1990, 1997; Eggleston and Lipcius 1992; Mintz *et al*. 1994; Schratweiser 1999). Octopuses, however, are notorious predators of crustaceans (Boyle *et al*. 1986; Mather 1991; Grisley 1996) and suspected predators of spiny lobsters, although remarkably few studies confirm this interaction. Most of our knowledge of octopus interactions with lobsters is anecdotal and based on reports from fishermen (Boyle 1997). Octopuses will consume constrained lobsters both in the laboratory and in the field (Joll 1977; Ambrose 1984), but their effect on natural lobster populations is unknown. In the only field study linking octopuses to lobsters, Anderson (1997) noted that the abundance of *Octopus tetricus* on rocky reefs in northeast New Zealand was unrelated to lobster (*Jasus edwardsii*) abundance or the abundance of eels, a major predator of this octopus. It has also been suggested that slipper lobsters (Scyllaridae) preferentially dwell with eels, which eat octopuses but rarely consume lobsters (E. Spanier, University of Haifa, Israel, pers. comm).

Octopuses may prey on lobsters, but both seek similar crevice shelters and mollusc prey. Observations of *O. briareus* (Hanlon 1983; Aronson 1986), *O. bimaculoides* (Ambrose 1982), *O. vulgaris* (Mather), *O. cyanea* (Van Heukelem 1983; Forsythe and Hanlon 1997), and *O. tetricus* (Anderson 1997) indicate that octopuses generally reside in cavities under rocks, sponges, and corals or in crevices on

reefs. These are the same habitats preferred by spiny lobsters wherever their distributions overlap (see Butler and Herrnkind 2000; Lipcius and Eggleston 2000 for reviews). As noted earlier, molluscs are the primary or secondary prey item sought by octopuses, just as they are for spiny lobsters (see Butler and Herrnkind 2000; Lipcius and Eggleston 2000 for reviews). The selective pressure on lobsters to avoid cohabitation with octopuses is therefore potentially great and is compounded by the possibility that octopuses prey on lobsters.

Chemical detection is one means by which prey avoid predators and is widely employed in aquatic systems. Chemical sensing of conspecifics promotes aggregation among juvenile and adult spiny lobsters, notably *P. interruptus* (Zimmer-Faust and Spanier 1987), *Jasus edwardsii* (Butler *et al.* 1999), and *P. argus* (Childress and Herrnkind 1996; Ratchford and Eggleston 1998, 2000). Whether lobsters respond to the chemical cues produced by potential predators is unknown, but chemical signals from octopuses can trigger dramatic behavioural responses in other crustaceans, most notably hermit crabs (Balasch and Mengual 1974; Ross and Boletzky 1979; Brooks 1991).

In this, our initial study of octopus–spiny lobster interactions, we conducted experiments to determine (1) whether den selection by juvenile spiny lobsters in mesocosms is influenced by chemical signals produced by octopuses and (2) whether the physical proximity of octopuses affects the field distribution of juvenile lobsters at several spatial scales. Juvenile *P. argus* did avoid dens emanating water-borne octopus odors, and the small-scale (<10 m) distribution of lobsters in nature was influenced by the presence of octopuses.

Methods

Laboratory Procedures

Juvenile Caribbean spiny lobsters were permitted to choose between two alternative shelter situations: (1) a shelter supplied with untreated seawater from a head tank (shelter + seawater) and (2) a shelter supplied with water from a head tank containing an octopus (shelter + chemical cue).

Juvenile lobsters (19–35 mm carapace length) and *Octopus briareus* Robson (95–267 g) were obtained from several shallow (<3m) sites in Florida Bay, Florida (USA), in June 1997. Octopuses and juvenile lobsters are common in the same hard bottom. We frequently found octopuses dwelling (often guarding eggs) in the same artificial crevice shelters that we deploy as shelters for juvenile lobsters (see, e.g. Butler and Herrnkind 1997). Lobsters were housed communally in a holding tank for no more than 14 days before each experimental trial; octopuses were caught 1–2 days before each trial and were kept singly in separate 75-L holding tanks. While in captivity, lobsters and octopuses were fed *ad libitum* a mixed diet of frozen shrimp and a variety of natural mollusc prey. Both lobsters and octopuses were released after the trials.

The experiments were conducted in two circular plastic arenas approximately 2.5 m in diameter and 0.3 m deep. Each arena received seawater through tubing connected to two separate head tanks (54 × 32 × 26 cm). Water flow from the tubing into each tank was approximately 1 ml/s. In one head tank we held an octopus to serve as

the source of our chemical-cue treatment. The other held only seawater. Both tanks were situated out of view, so visual cues were not available to the test lobsters. Each of the two water lines entering each experimental arena was attached to one of two lobster shelters, creating two treatment conditions (1) shelter + seawater and (2) shelter + chemical cue. Each shelter consisted of two three-hole concrete partition blocks (30 × 15 × 7.5 cm), which are accepted by lobsters as suitable shelters in the field (Butler and Herrnkind 1997).

In a randomized block design, we individually tested 30 juvenile lobsters, 10 lobsters for each of the three octopuses we used as sources of chemical cues. Before each trial, a single octopus was placed in the chemical-cue head tank for 24 hr. Then a single lobster was introduced into the centre of the arena, and its position in the arena was observed after 12 and 24 hrs. The shelter that housed the lobster after 24 hr was designated the preferred shelter. The 24-hr time period was chosen on the basis of longer preliminary trials, which showed that the majority of lobsters tested had not chosen a 'permanent' den (i.e. one in which they would remain for several days) by 12 hr but that nearly 100% had done so after 24 hr.

A 2-way log-linear contingency-table analysis was used to determine whether the two shelter treatments differed significantly in occupancy by juvenile lobsters. The planned 3-way (shelter use × shelter type × individual octopus) log-linear contingency-table analysis, which permitted a test of the potential 'block effect' of individual octopuses, was not appropriate for these data because >20% of the cells contained values <5, which violates an assumption of this test. Inspection of the data revealed no obvious individual-octopus effect (i.e. only 7% difference among octopuses).

Field Procedures

We tested the effect of octopuses on the distribution of juvenile lobsters within dens at several spatial scales using field manipulations of artificial den spacing at five test sites 30–50 m offshore of Grassy Key in Florida Bay, Florida (USA). The sites were typical spiny-lobster nursery habitat, that is, hard-bottom areas that were 2–3 m deep. At each site we placed 18 six-hole concrete shelters (60 × 30 × 15 cm) in six sets of three, each set spaced 10 m from the next (Fig. 1). We arranged the three shelters forming each set in a triangular formation and randomly assigned block spacing, so that the shelters in three sets were spaced 2 m apart and those in the other three sets were spaced 0.5 m apart. This arrangement allowed us to test the cohabitation of lobsters and octopuses at five spatial scales: (1) < 0.1 m, within the same hole of a shelter; (2) 0.1 m, a different hole but within a shelter;
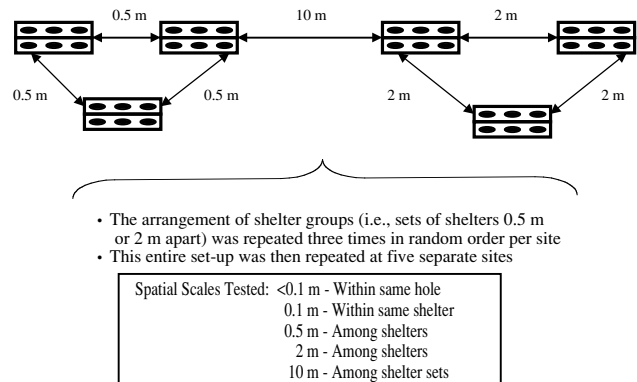
Fig. 1. The design of the experiment used to measure cohabitation patterns by juvenile lobsters and octopuses within artificial shelters deployed in the field at five different sites in the Florida Keys, Florida. Cohabitation was investigated at five different spatial scales where dens were < 0.1 m, 0.1 m, 0.5 m, 2 m, and 10 m apart.

(3) 0.5 m, among shelters within a closely spaced set; (4) 2 m, among shelters within a widely spaced set; and (5) 10 m, among sets of shelters.

We revisited each site 14 days after deployment to allow time for both octopuses and lobsters to colonize the shelters. At that time, divers recorded the presence and absence of octopuses and lobsters within each shelter hole, shelter, and set of shelters. All lobsters were caught and measured. A chi-square goodness-of-fit test or Fisher's exact test (for smaller sample sizes) was used to determine whether lobsters and octopuses co-occurred randomly at each of the five spatial scales. We also calculated several indices of species association (Jaccard's, Ochai, Dice) to describe the lobster-octopus association at each spatial scale. All these indices yielded similar results, so only the results of the Ochai index are reported. Index values approaching '1' indicate positive association, and those near '0' indicate negative association.

Results

In our laboratory tests, juvenile spiny lobsters responded to octopus chemical cues. Significantly more lobsters chose shelters without the chemical cue ($G = 5.75$, df = 1, $P = 0.025$; $n = 26$), indicating an avoidance response to *Octopus briareus*. Several lobsters actually reversed their direction after initially heading into a shelter emanating the octopus scent.

We encountered 112 juvenile lobsters and 18 octopuses during surveys of 540 artificial dens at our five field sites. Lobsters ranged in size from 20.9 to 36.7 mm CL; we did not measure the octopuses. The presence of an octopus significantly influenced the small-scale distribution of juvenile lobsters in the artificial dens (Fig. 2). Lobsters and octopuses were never found within the same crevice (<0.1 m; $\chi^2 = 19.5$, df = 32, $P < 0.0001$) and rarely within the same artificial shelter (i.e. within 0.1 m; $\chi^2 = 13.9$, df = 28, $P = 0.0002$) or in adjacent shelters whether closely (Fisher's exact test: $n = 14$, $P = 0.0174$) or widely (Fisher's exact test: $n = 11$, $P = 0.0137$) spaced. In contrast, the co-occurrence of lobsters and octopuses within sets of shelters spaced 10 m
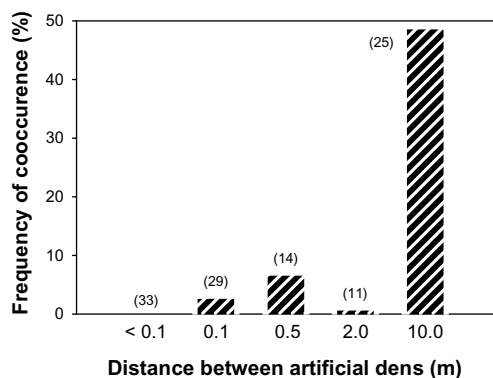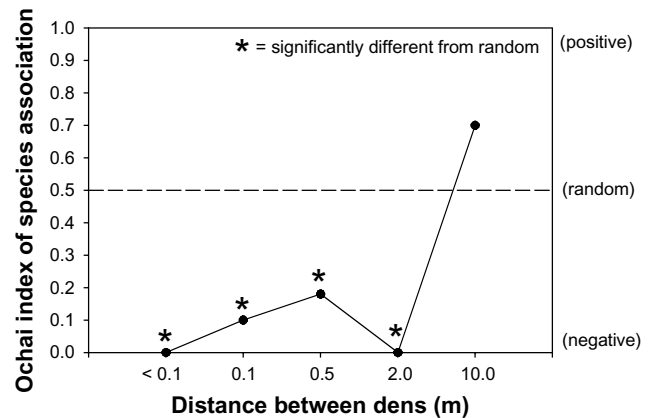
Fig. 3. A plot of the Ochai index describing lobster-octopus association for the five spatial scales (i.e. interden distance) tested. Values approaching '1' indicate a positive association, and those near '0' indicate a negative association. Each value significantly different from a random association at the $\alpha = 0.05$ level is indicated by a '*.'

apart was not significantly different from random ($\chi^2 = 0.02$, df = 24, $P = 0.8908$). These differences were consistent among sites. These results from the goodness of fit tests verify the distributions implied by the association indices (Fig. 3), which indicate negative associations at < 0.1-m, 0.1-m, 0.5-m, and 2-m scales and random association at 10 m.

Discussion

Anecdotal accounts of octopuses preying on lobsters abound (e.g. see Boyle 1997), yet we are unaware of any peer-reviewed publications on the subject. Although octopuses are potential lobster predators, they also occupy similar crevice shelters and eat similar prey (Ambrose 1982, Aronson 1986, Anderson 1997), thereby increasing the possibility for strong interactions. In the present study, we tested for effects by Caribbean reef octopus chemical cues on shelter choice by juvenile Caribbean spiny lobsters and for effects by octopuses on the spatial distribution of lobsters in the field. Our results show that juvenile Caribbean spiny lobsters are sensitive to octopus chemical cues and avoid shelters emanating such chemicals; 73% preferred shelter without octopus scent. Chemoreception is an effective means by which many crustaceans detect predators (e.g. see Brooks 1991) and prey (see, e.g. Zimmer-Faust 1989) in aquatic systems, although flow and substrate characteristics influence turbulence and, therefore, signal transmission (Weissburg and Zimmer-Faust 1993). Because octopuses and lobsters inhabit similar shelter types, the chance of encounter is potentially great unless lobsters detect octopus presence at sufficient distance to avoid the shelter.

Our field experiments demonstrated that lobsters and octopuses are rarely found in shelters less than 2 m apart,

Fig. 2. Frequency of co-occurrence between juvenile spiny lobsters and octopuses in artificial dens separated by five distances: < 0.1 m, 0.1 m, 0.5 m, 2 m, and 10 m apart. The numbers in parentheses near each bar in the histogram are the numbers of dens in which either a lobster or an octopus was observed.

although their occupancy of shelters 10 m apart is random. Avoidance of crowding could explain the reluctance of lobsters to share single dens or very closely spaced ones with octopuses, but because lobsters were also rarely found in dens within 0.5 m or even 2 m of octopuses, interference competition and predator avoidance are more likely explanations.

Octopuses might also have reduced lobster numbers near their dens by preying on their lobster neighbours. Octopuses would have to consume many lobsters to produce this effect, yet octopus-den shell middens at the experimental sites did not contain any lobster shells. Nevertheless, our study was not designed to distinguish between the independent influences of predation and competition, which may not be mutually exclusive. In fact, combined, they provide a particularly powerful selective agent for shaping lobster responses to octopuses.

Because lobsters avoid octopus chemical cues, the two would become 'overdispersed' relative to one another under natural conditions where shelters are abundant, but in some hard-bottom areas near the Florida Keys, crevice shelters suitable for lobsters are sparse and limit local lobster abundance (Butler and Herrnkind 1997). In addition, approximately 300 km^2 of south central Florida Bay have experienced a massive loss of crevice habitat in response to cyanobacteria blooms that killed most sponges in the region. There, shelter for juvenile lobsters—and presumably octopuses—may be limited, certainly more limited than before the blooms (Butler *et al.* 1995; Herrnkind *et al.* 1997). If octopuses are similarly affected by these circumstances, then the strong interaction between juvenile lobsters and octopuses is likely to be accentuated in regions like central Florida Bay, where shelters are few. Competition for scarce shelters may be fiercer and predation on lobsters may increase for several reasons.

First, encounter rates between lobsters and octopuses will increase if shelters are few, but so might lobster aggregations. Octopuses forage both day and night either by pouncing on prey caught in the open or by probing into crevices with their tentacles and extracting the trapped prey (Forsythe and Hanlon 1997). Juvenile lobsters aggregate in shelters in response to chemical cues released by conspecifics (Ratchford and Eggleston 1998, 2000; Butler *et al.* 1999), and aggregation reduces predation risk in some species (Butler *et al.* 1999; but see Childress and Herrnkind 1994, 1996,1997). The effectiveness of octopus as predators in the face of lobster aggregation is unknown.

The competitive implications of the simultaneous consumption of molluscs by octopus and lobsters are obvious, although the overlap between the two in prey size and prey selectivity has not been investigated. Less obvious, but potentially important, are the indirect effects of octopus and lobster competition for molluscs, especially where shelters are few and the competitors are forced into close proximity. If local lobster or octopus densities are high, mollusc densities will diminish through consumption. Although some octopus species feed selectively, many are 'switching predators' and consume prey in proportion to their abundance (Joll 1977; Ambrose 1984; Vincent *et al.* 1998; Dodge and Scheel 1999; Grubert *et al.* 1999). With fewer molluscs to consume, octopus predators will increase their consumption of crustaceans—shrimps, crabs, and lobsters. Thus, by competing with octopus for mollusc prey, lobsters may indirectly increase their own risk of mortality from octopuses

This initial study of octopus–spiny lobster interactions leaves much to be resolved. Nonetheless, we conclude thus far that octopuses can influence, by means of chemical signals, the selection of shelters by juvenile Caribbean spiny lobsters and consequently the small-scale spatial distribution of lobsters in nursery habitat. In the future, we hope to explore in more detail the complicated predator-competitor associations between these species, focussing on their possibly subtle indirect interactions.

Acknowledgments

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